ANATOMY AND PALAEOECOLOGY OF *PSEUDOFRENELOPSIS* AND ASSOCIATED CONIFERS IN THE ENGLISH WEALDEN

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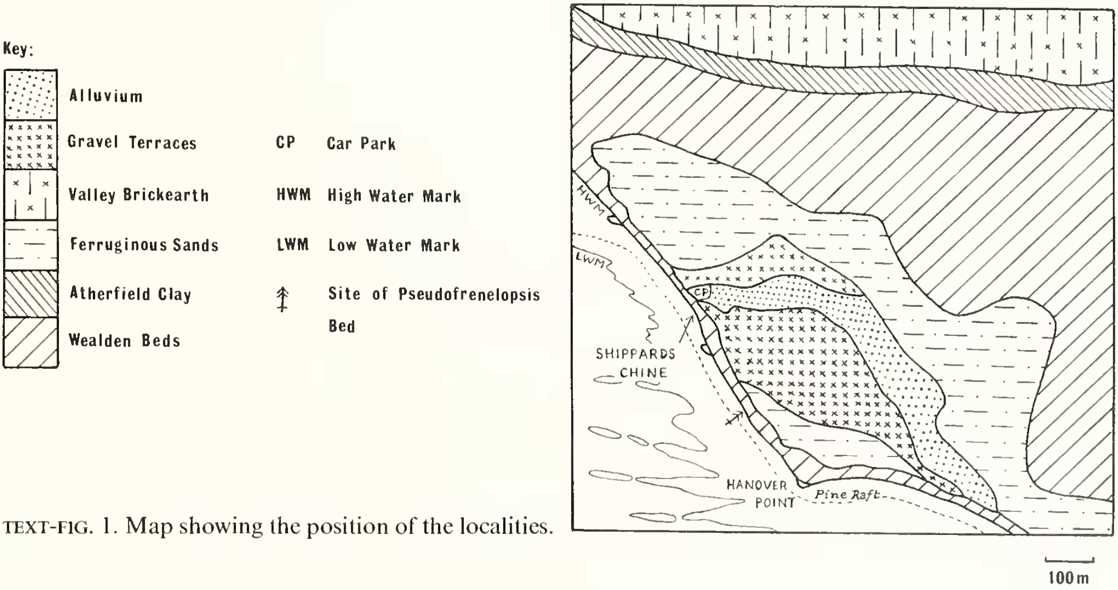
ABSTRACT. Among the preserved woody debris associated with the fossil conifer *Pseudofrenelopsis parceramosa* (Fontaine) Watson from a deposit in the Wealden of the Isle of Wight, three wood types have been characterized. One corticated twig with internal structure preserved, has provided good evidence that one of the woods belonged to *Pseudofrenelopsis*. This wood, which is of the *Protopodocarpoxylon* type, is represented by both mineralized and fusainized specimens and a comparison of these supports the view that the fusain was formed by charring. A preliminary analysis of the woody debris at the nearby 'Pine Raft' deposit reveals a similar but not identical assemblage of woods. The palaeoecological implications of the results are discussed.

THE material on which the work is based comes from the Brook Formation, believed to be of Barremian age (Hughes, 1975). Most of the material was collected from a site about midway between Shippard's or Compton Grange Chine* and Hanover Point. This site, referred to previously by Oldham (1976) and Alvin *et al.* (1978) is exposed in the cliff and also on the shore at low tide some 20 m to the west (text-fig. 1). We refer to this as the Shippard's Chine site as Shippard's Chine is the nearest access point.

The famous 'Pine Raft' logs lie at Hanover Point about 200 m to the south-east and some 50 m lower down the section.



TEXT-FIG. 1. Map showing the position of the localities.

* The locality was referred to as Compton Grange Chine by Alvin *et al.* (1978), but the name Shippard's Chine is used on Ordinance Survey Sheet No. SZ38. The names are given as alternatives by White (1921).

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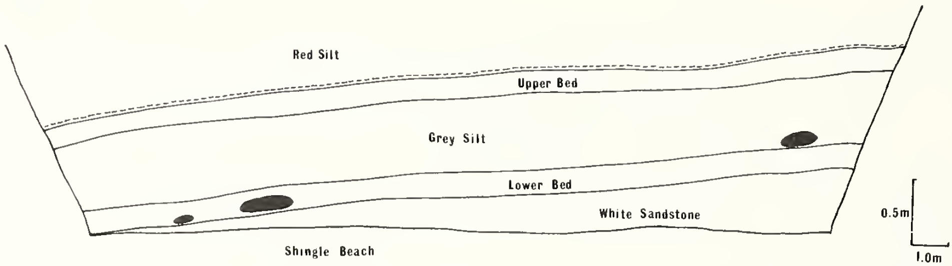
DETAILS OF THE LOCALITIES

The Shippard's Chine site (text-fig. 2).

The cliff exposure shows the organic material concentrated in two distinct layers which we have designated upper and lower beds. These are separated by a zone of some 70 cm of grey silt in which organic remains are much less frequent. The matrix throughout is very similar, mainly a silt and fine sand with a small clay fraction; it is finer in the upper bed than in the lower. The lower bed which is about 30 cm thick, resting on a greyish-white sandstone, contains an abundance of compressed twigs, wood fragments and also logs up to approximately 40 cm in diameter. One aggregation of massive material measured about 1·5 m across. Parts of the bed are laminated and packed with plant debris; others show poorly developed current bedding with sparser remains. The upper bed is about 25 cm thick and lacks massive logs; it is otherwise similar, but apparently contains a larger proportion of more finely divided material in a more or less oxidized state. Immediately above lies a thin brown, organic-rich layer without well preserved plants, which we suggest may represent a palaeosol. We envisage the whole deposit as representing a stream channel in which flow rate was variable and which progressively silted up. The two beds probably represent depositions of forest floor debris, perhaps deriving from bank erosion upstream.



TEXT-FIG. 2. Diagram of the cliff exposure of the Shippard's Chine *Pseudofrenelopsis* beds. Sides are covered by slumped material from the cliff. Solid black represents fossil logs or rafts of logs.

Both beds contain an abundance of compressed shoots of *Pseudofrenelopsis parceramosa* with well-preserved cuticles, together with male cones (*Classostrobus comptonensis* Alvin *et al.*) believed to belong to the same plant. Female cone scales of the *Hirmeriella* type, not yet described, have also been collected. Present as compressed shoots, but comparatively infrequent, is another conifer identified provisionally as *Brachyphyllum obesum* Heer. Among the remains with preserved cuticles, apart from these two conifers, we have found only occasional fragments of Bennettitalean leaves. However, the deposit contains an abundance of decorticated twigs and wood fragments, often with well preserved structure. Most of the twigs and logs are compressed with little cellular detail preserved, but occasionally large logs have their centres mineralized in silica and many axes are partially pyritized. One single specimen of a corticated twig has been recovered showing clearly the morphological and cuticle characters of *Pseudofrenelopsis parceramosa* and with much internal structure (Pls. 111, 112). This unique specimen showed evidence that it may have been charred before some pyritization of the internal tissues occurred. The extreme rarity of twigs preserved in this manner may be because fragile charred twigs would tend to be destroyed during transportation.

Pieces of fusain up to about 3 cm in diameter and representing secondary wood are common throughout the lower bed and only slightly less so in the upper. These generally have a rounded, water-worn appearance. We interpret this material as fossil charcoal chiefly on the basis of its physical and optical properties. Like Harris (1957, 1958), Scott and Collinson (1978) and others, we believe it to represent the product of periodic vegetational fires.

Much of the material examined, regardless of the mode of fossilization, has shown evidence of some decay before preservation. Secondary wood tracheids, including those of the structurally preserved *Pseudofrenelopsis* twig, often show a spiral system of cracks or fissures strongly reminiscent of a soft-rot type of degradation (Pl. 107, fig. 4; Pl. 111, fig. 7). Structures which we believe are fungal hypae have frequently been observed both in ray cells and in tracheids and in some cases they have been seen passing through tracheid walls (Pl. 108, fig. 5). Such penetration observed in a specimen preserved as fusain, as in the example illustrated, must, we believe, indicate that the fungal growth occurred before charring, probably in the forest floor litter.

The 'Pine Raft' site.

The massive logs exposed at low tide and known for many years as the 'Pine Raft' are mineralized in carbonate. They lie in sandstone in which there are layers of grey silt rather similar in appearance to the Shippard's Chine matrix but harder and somewhat calcareous. This matrix contains little or no cutinized plant material but there is often an abundance of wood fragments many of which are again preserved as fusain.

METHODS

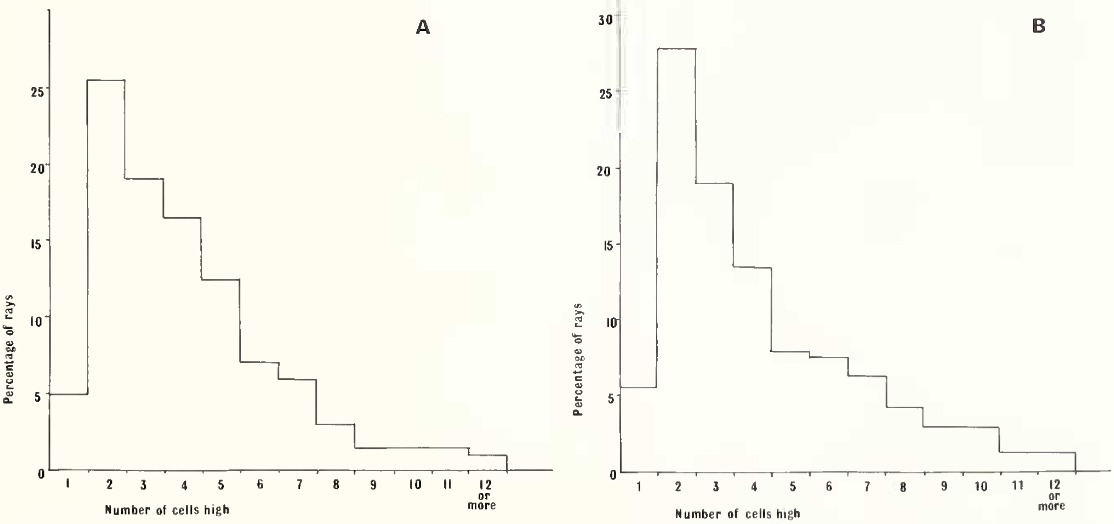
Material mineralized in silica or carbonate has been studied from both rock sections and peels. Pyritized, fusainized and compressed lignitic material has been examined by scanning electron microscopy. Specimens for SEM were freshly cleaved by means of a fine, sharp scalpel under a low-power stereoscopic microscope. With pyritized and fusainized samples, attempts to display transverse, radial longitudinal and tangential longitudinal planes were usually successful, but with compressed wood only transverse and radial longitudinal planes could be displayed; transverse fractures of such material, however, yield little or no useful information. The structurally preserved corticated twig was snapped transversely to yield a cross-section, and one resultant portion was cleaved in the radial longitudinal plane. All specimens for SEM were stuck to stubs with 'Durofix' and sputter coated with gold.

DESCRIPTIONS OF THE WOODS FROM THE SHIPPARD'S CHINE SITE

1. *Silicified material* (Pls. 106, 107; text-fig. 3A)

Three specimens have been examined: two representing the mineralized cental portions of logs *in situ*, and the third a log, some 70 cm in diameter, found lying on the shore at the foot of the exposure. All showed identical structure, though the preservation was somewhat variable. One slide in the British Museum (Natural History) Collection (V8387) labelled 'Coniferous wood, Brook, Isle of Wight' we also identify as the same.

Transverse section. Secondary wood consisting of tracheids and parenchymatous rays only. Growth rings distinct but uneven, represented by narrow zones of smaller, late wood tracheids alternating with usually much broader zones of larger, early wood tracheids; gradation rather abrupt. Some tracheids, especially in late wood, and ray cells often filled with a dark (?resinous) deposit. Tracheids (excluding late wood) about 520/mm^2; lumen rounded; wall about 7 μm thick. Resin ducts absent. Horizontal cross walls of septate tracheids occasionally seen in late wood.



TEXT-FIG. 3. Histograms showing the percentages of rays of different heights. A. Silicified wood. Based on 250 rays in the best preserved specimen. B. Fusain Type I. Based on 238 rays from the best preserved specimen.

Tangential longitudinal section. Tangential pitting common in late wood, small, uniseriate (rarely biseriate alternate), generally spaced but occasionally contiguous, rare in early wood. Rays mainly uniseriate, 1–15 (mode 2, *c*. 60% 2–4) cells high, occasionally partially biseriate. About 30 rays per mm^2. Ray cells 16–29 μm high, 13–27 μm wide, thin-walled.

Radial longitudinal section. Tracheid pitting predominently uniseriate and contiguous, with borders flattened and often thickened where in contact; sometimes more spaced; occasionally biseriate (opposite or rarely alternate). Pits 19–24 μm in diameter, aperture usually slightly elliptical. Ray cells rectangular with vertical end walls; walls thin, uniform, not obviously pitted on end and horizontal walls. Cross-field square to slightly elongated horizontally. Cross-field pits cupressoid (1–) 4–10 (–16) per field, crowded but usually not in contact, arranged in 2–3 (–4) horizontal rows; pits about 7·0 μm in diameter, round, with small obliquely orientated elliptical apertures about 2×1 μm.

This wood is discussed below.

2. *Fusain.*

Altogether twenty-six specimens of fusain have been examined. These were either collected in the field from different parts of the exposure or recovered from broken down blocks of matrix in the laboratory. The degree of preservation was variable: most samples showed well-preserved structure which we were able to examine in three planes of fracture. A few, however, were too poorly preserved, either because of shattering or sometimes apparently because of a high degree of biological decay having occurred, presumably before charring. Many specimens were partially pyritized.

Three anatomically different types of wood have been recognized. These are described below as Types I–III. By far the most frequent was Type I of which seventeen specimens were certainly identified and three doubtfully. Five specimens of Type II were seen and only one of Type III. The identity of Type I with the silicified wood is discussed following the description.

Type I (Pl. 107; Pl. 108, figs. 1, 2; text-fig. 3B)

Transverse section. Secondary wood consisting of tracheids and parenchymatous rays only. Growth rings distinct, irregular, represented by narrow zones of small, late wood tracheids alternating with much broader zones of early wood; gradation rather abrupt. Tracheids, excluding late wood, about 1250/mm^2, lumen rounded; wall about 3 μm thick. Bordered-pitted transverse walls of septate tracheids occasionally seen in late wood.

Tangential longitudinal section. Tangential pitting common in late-wood, small uniseriate, spaced or contiguous, rare in early wood; pits *c*. 10 μm in diameter. Rays mainly uniseriate, occasionally partially biseriate, 1–14 (mode 2, *c*. 60% 2–4) cells high. About 60 rays per mm^2. Ray cells 13–27 μm high, 10–27 μm wide, thin-walled.

Radial longitudinal section. Tracheid pitting predominently uniseriate, contiguous, with borders flattened and thickened in plane of middle lamella where touching, sometimes spaced, rarely biseriate (opposite). Pits 11–20 μm in diameter; aperture slightly elliptical. Ray cells rectangular with vertical end walls; walls thin, uniform, apparently not pitted on horizontal and end walls. Cross-field square to slightly elongated horizontally. Cross-field pits cupressoid, (2–4) 4–10 (–17) per field, about 4·5–6·0 μm in diameter, crowded but round, not angular, arranged in 2–3 (–5) horizontal rows, with small (*c*. 1×2 μm), elliptical, obliquely orientated apertures.

Comments. Type 1 wood is closely similar in virtually all structural characters to the silicified wood. We have not observed alternate biseriate pitting, but this is only rarely seen in the silicified material. The cross-fields in the fusain are occasionally somewhat higher, with up to five horizontal rows of pits; this might be expected if the fusain included twig wood where ray cells may be higher than in

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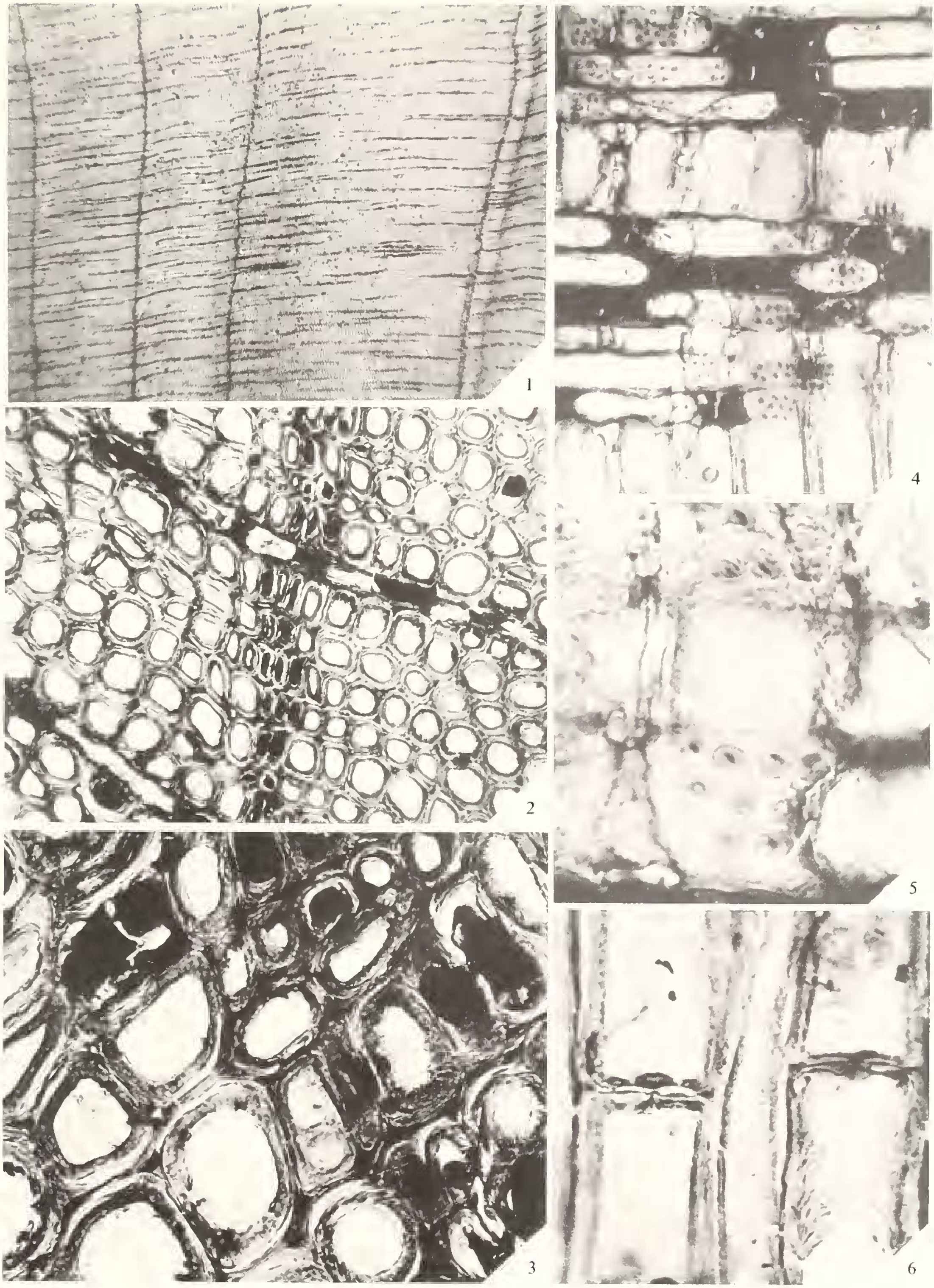
EXPLANATION OF PLATE 106

Specimen from Shippard's Chine, Isle of Wight. *Pseudofrenelopsis parceramosa* (Fontaine) Watson (Silicified wood). 1. T.S. showing irregular growth rings. V60204. ×10. 2. T.S. showing growth rings. V60204. ×216. 3. T.S. at growth ring showing typical preservation; the transverse wall of a septate tracheid is seen just below the centre. V60204. ×520. 4. R.L.S. showing rays and cross-field pitting. V60205. ×280. 5. R.L.S. showing detail of cross-field pitting. V60205. ×1000. 6. T.L.S. showing bordered-pitted horizontal walls of two septate tracheids. V60206. ×520.



ALVIN *et al.*, *Pseudofrenelopsis*

TABLE 1. Comparison of the silicified wood and fusain Type I

	Silicified	Fusain	Per cent reduction in linear dimension
No. of tracheids per mm²	520	1250	35
Tracheid tang. diam.	42 μm	31 μm	26
Tracheid wall	7 μm *(5 μm)	3 μm	57 (40)
Rays per mm²	30	60	29
Ray cell ht.	30 μm	20 μm	33
Ray cell width	25 μm	18 μm	28
Tracheid pit diam.	20 μm	15 μm	25
Cross-field pit diam.	7 μm	5 μm	29

* Corrected for gaps in wall layer probably produced by partial decomposition before preservation.

trunk wood of the same species (Schweingruber, 1978). However, in cell dimensions (Table 1) there are striking differences: in the fusain there are more than twice as many tracheids per sq. mm. and linear dimensions of cell lumina and pits are of the order of 30% less; tracheid wall thickness is 40–50% less.

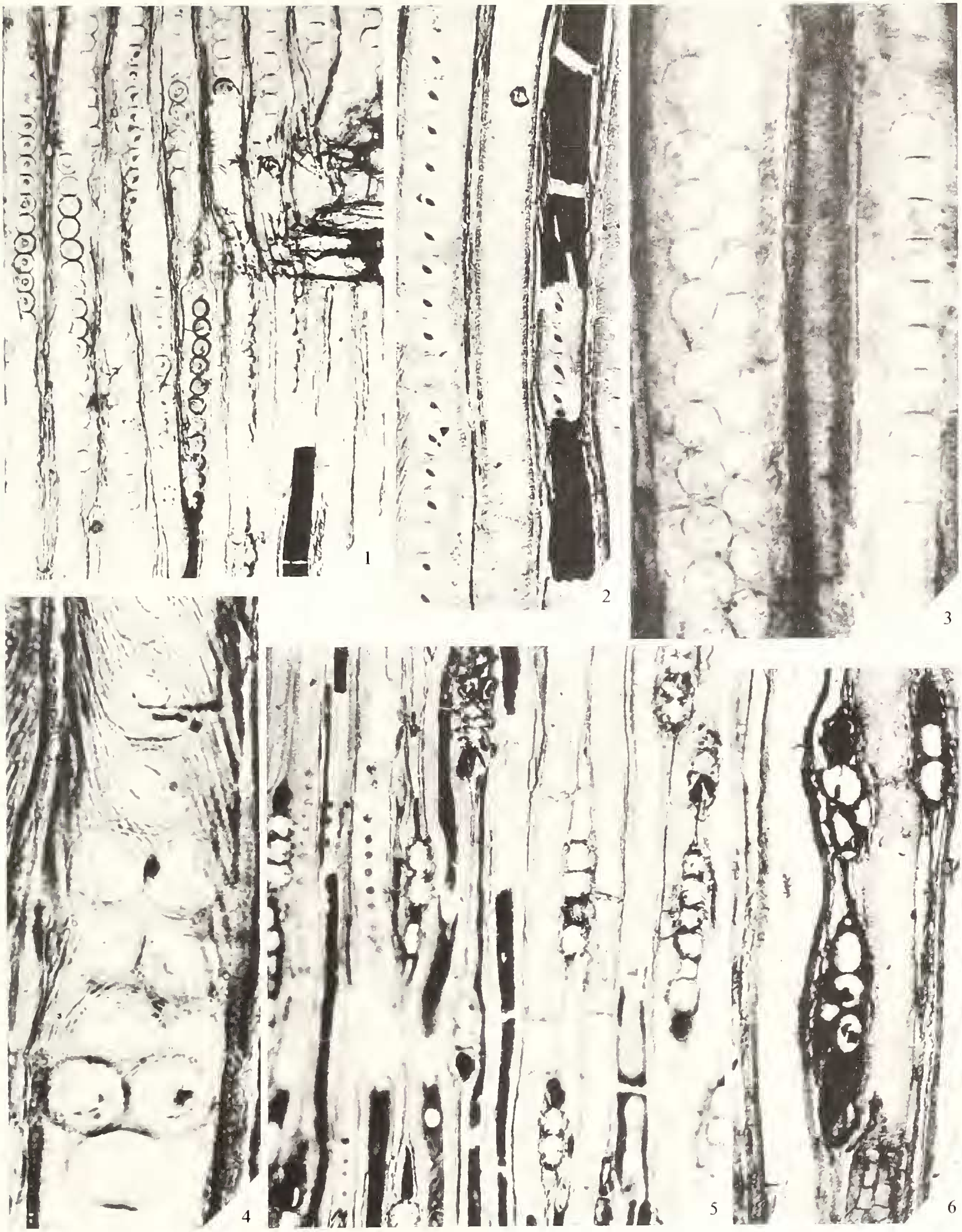
Such dimensional differences may reasonably be attributed to shrinkage caused by charring. Harris (1957), on the basis of experimentally produced charcoals, estimated shrinkage to be 10–30%. More recently, McGinnes *et al.* (1976), using *Quercus alba*, have shown that shrinkage varies with temperature of charring and that shrinkage of cell wall thickness is greater than that of the cell lumen. At 400 °C tangential vessel diameter shrank by 25·6% in early wood and 22·6% in late wood; at 800 °C the comparable figures were 38·9% and 25·8%. Wall thickness of fibres shrank by 36·5% at 400 °C and by as much as 50·8% at 800 °C. The difference in tracheid wall thickness between our silicified and fusainized wood is as much as 57% if the wall thickness in the former is taken as 7 μm. However, the appearance of the walls suggests that they may have become distorted by partial decomposition in such a way that the inner layer appears to have pulled away somewhat from the outer, often leaving a space (Pl. 106, fig. 3). If this space is excluded, the average wall thickness measures about 5 μm and the thickness in the fusain then represents a 40% shrinkage, still greater than the shrinkage of lumen dimensions.

The comparison between the two differently preserved fossil woods is thus entirely consistent with the view that the fusain was produced by charring.

The wood, on the basis of its general features falls into the form-genus *Protopodocarpoxylon* Eckhold.

EXPLANATION OF PLATE 107

Specimen from Shippard's Chine, Isle of Wight. *Pseudofrenelopsis parceramosa* (Fontaine) Watson (Silicified wood). 1. R.L.S. showing typical pitting. V60205. ×136. 2. R.L.S. showing tracheid with dark contents. V60205. ×210. 3, 4. R.L.S. showing biseriately pitted tracheids. 3, V8387. ×400; 4, V60205. ×600. 5. T.L.S. showing rays, septate tracheids and tangential pitting. V60206. ×136. 6. T.L.S. showing two partially biseriate rays. V60206. ×216.



ALVIN *et al.*, *Pseudofrenelopsis*

Type II (Pl. 109, figs. 3–8; text-fig. 4A)

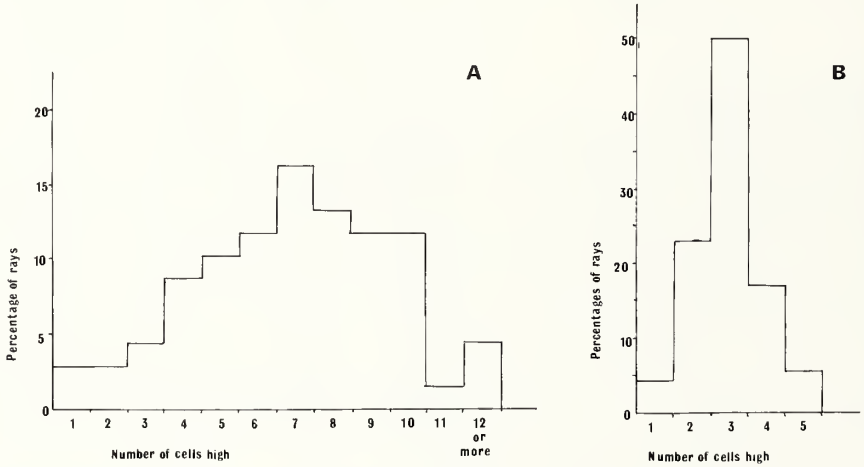
Transverse section. Secondary wood consisting of tracheids and parenchymatous rays only. Growth rings present, irregular, represented by narrow zones of small late-wood tracheids alternating with very much broader zones of early wood; gradation abrupt. Tracheids, excluding late wood, about 1770/mm², lumen angular, square to hexagonal; wall about 2 μm thick. Resin ducts absent.

Tangential longitudinal section. Tangential pitting sparse in late wood, small, uniseriate, spaced. Rays uniseriate, (1–) 4–10 (–13) cells high (mode 7); about 65 rays per mm². Ray cells 8–17 μm high, 7–13 μm broad, probably with rather thick walls.

Radial longitudinal section. Tracheid pitting uniseriate, occasionally biseriate (opposite), usually spaced, rarely contiguous. Pits 16–20 μm in diameter; aperture generally slightly elliptical. Cross-field square, with 1–2 large, round, dacrydioid pits (when two, arranged either horizontally or diagonally); pit with narrow, even border about 0·8 μm wide; aperture 5–10 μm in diameter.

Comments. Type II wood is probably classifiable in the form-genus *Circoporoxylon* Kräusel (1949) on the basis of its circular, narrowly bordered cross-field pits and abietinean tracheid pitting. It is clearly distinguished from Type I by both of these important characters as well as several others, including the thinner walled tracheids and their different shape in transverse section and ray cell number frequency.

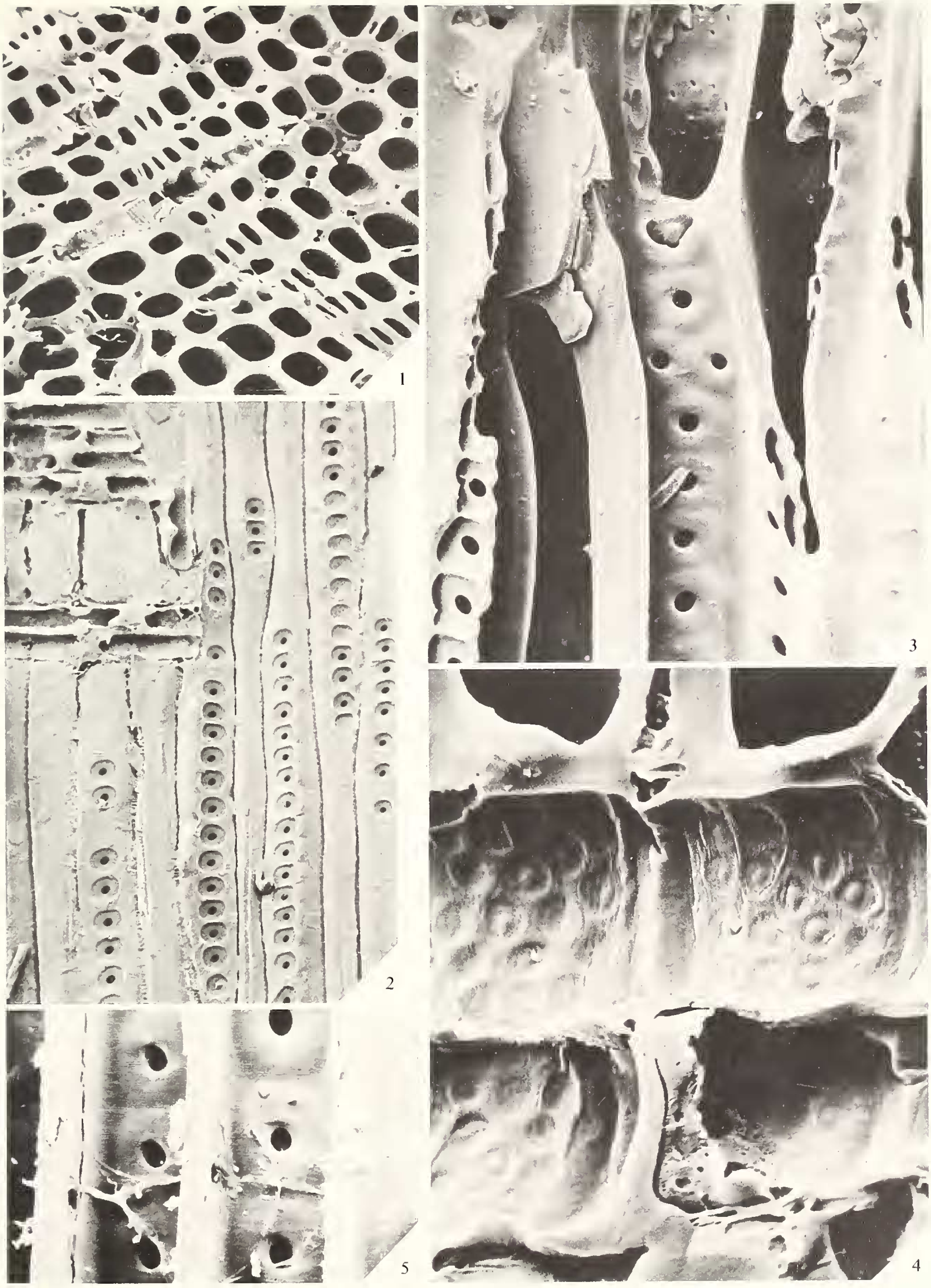
A remarkable feature of this fusain is the infrequency with which the rays fracture in the radial longitudinal plane. We believed at first that this might have been due to the ray cells having very thick



TEXT-FIG. 4. Histograms showing the percentages of rays of different heights. A. Fusain Type II. Based on sixty-eight rays from the best preserved specimen. B. Fusain type III. Based on seventy rays.

EXPLANATION OF PLATE 108

All specimens from Shippard's Chine, Isle of Wight. *Pseudofrenelopsis parceramosa* (Fontaine) Watson (Fusain Type I). 1. T.S. at growth ring. ×240. 2. R.L.S. showing typical tracheid pitting; a partially pyritized specimen with pits seen as from plane of the middle lamella. ×235. 3. R.L.S., pits variously seen due to irregular fracture; at top, cross-field pitting seen from the tracheid side. ×600. 4. R.L.S. with cross-field pitting seen from the ray cell side. ×1350. 5. R.L.S. showing apparent fungal hyphae penetrating tracheid walls. ×850.



ALVIN *et al.*, *Pseudofrenelopsis*

walls. Tangential fractures show the ray cells with apparently thick and often irregular walls (Pl. 109, figs. 4, 5). However, it is difficult to determine if this may not represent a deposit on the inside of the cells which, perhaps because of charring, has become fused to the true wall. Even the pit membranes (Pl. 109, fig. 4) appear extremely thick. Deposits are occasionally seen in tracheids, but are fairly clearly delimited from the wall (Pl. 109, fig. 5).

It seems likely that the plant to which this wood belonged was taxonomically rather far removed from that represented by Type I. Except for the absence of wood parenchyma, the wood is not dissimilar to that of some modern Podocarpaceae, particularly perhaps *Dacrydium*.

Type III (*Based on one specimen only*; Pl. 110, figs. 1–3; text-fig. 4B)

Transverse section. Secondary wood consisting of tracheids and parenchymatous rays only. Growth rings indistinct. Tracheids polygonal to rounded, about 3140/mm^2; wall about 2 μm thick. Resin ducts absent.

Tangential longitudinal section. Tangential pitting sparse in late wood, small, uniseriate, spaced. Rays uniseriate, occasionally partly biseriate 1–5 (mode 3; 73% 2–3) cells high; about 90 rays per mm^2. Ray cells 13–18 μm high, 10–16 μm broad.

Radial longitudinal section. Tracheid pitting (apparently sparse), uniseriate, not or rarely contiguous. Pits about 12 μm in diameter; aperture slightly elliptical. Cross-field approximately square, with 1–4 pits, variously arranged; pits cupressoid, round, 2·5–5·0 μm in diameter with oblique, elliptical apertures about 3·0 × 1·0 μm.

Comments. We have not been able to describe this wood as fully as the others because only one specimen was found. It has characters which clearly distinguish it from the others, chiefly the different cross-field pitting and different ray cell number frequency. We have seen very few tracheid pits, but they seem to be abietinean in arrangement. The wood is probably classifiable in the form-genus *Cupressinoxylon* Goeppert.

3. *Structurally preserved twig of* Pseudofrenelopsis parceramosa (Pls. 111, 112).

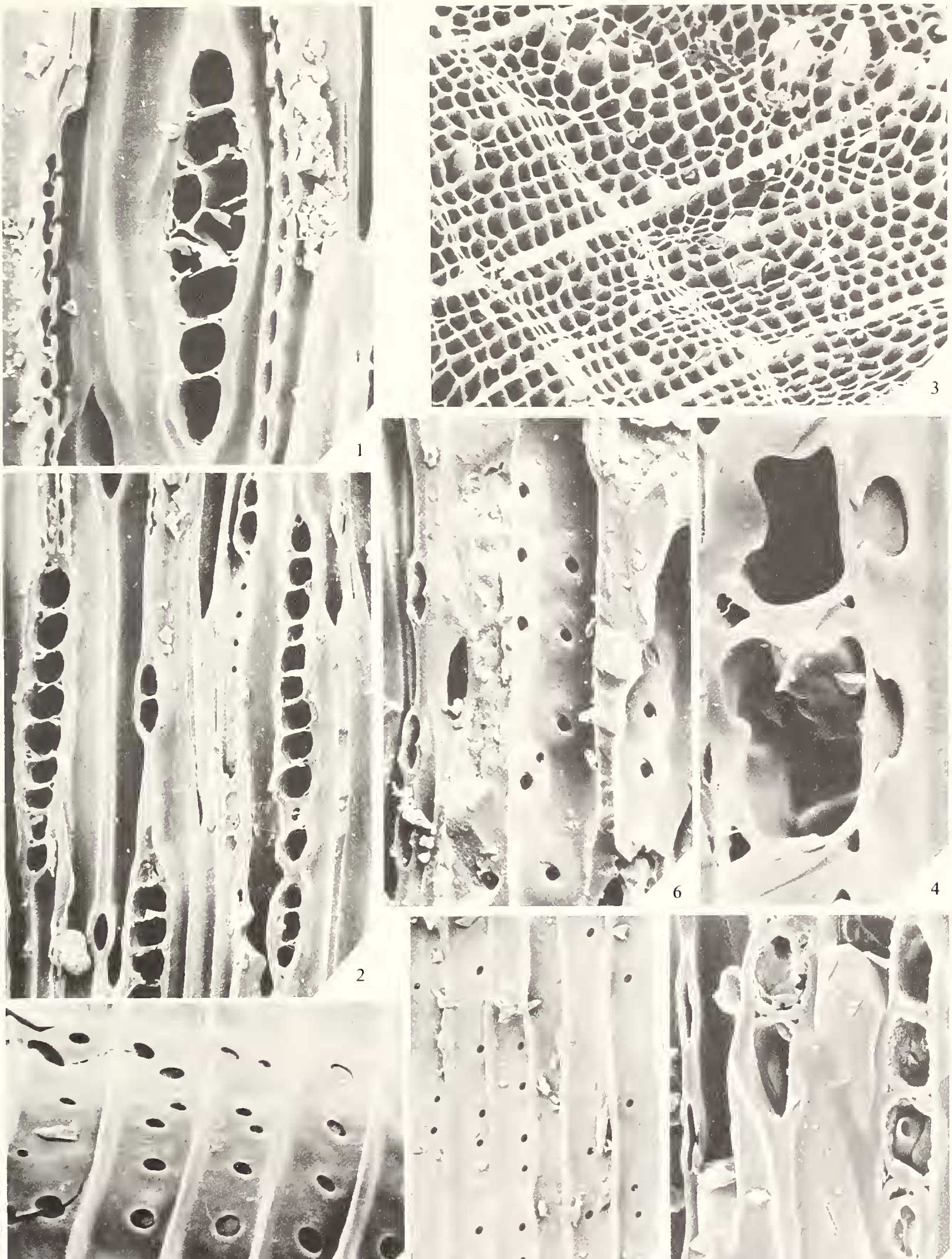
This specimen, comprising one node and portions of the internodes above and below, measured 9 mm in length, 4 mm in diameter (in plane of compression) and 2 mm thick (at right angles to plane compression). The tissues vary greatly in their degree of compression: the pith, much of the wood and the hypodermal fibrous bundles show little or no distortion, though some of the wood, especially at the top and bottom of the cylinder in relation to the compression plane, has shattered and compacted (Pl. 111, figs. 2, 5). Mineralization in iron pyrites is virtually confined to the pith which is preserved without compression. Presumably mineral precipitation occurred at an early stage of burial before compression. The fractured cell walls, particularly of the wood, the hypodermal fibres and the epidermis have a homogeneous appearance similar to that of charcoal and fusainized wood (e.g. Pl. 111, figs. 3, 5; Pl. 112, fig. 1). Some degree of decay had probably occurred before charring: ray cells sometimes show what may be fungal hyphae (Pl. 112, fig. 5) and the tracheid walls often show oblique fissues reminiscent of a soft-rot type of decay. If we are right in believing that this specimen was charred, such biological degradation must have occurred beforehand. The cortex, apart from bundles of thick-walled hypodermal cells and occasional isolated or small nests of possible stone-cells (Pl. 111, fig. 4), is completely shattered (Pl. 112, fig. 1). It appears to have consisted of a broad zone of thin-walled cells. It is the collapse of this tissue which accounts almost entirely for the 50% compression of the twig as a whole. Beneath the epidermis, with its extremely thick outer walls (Pl. 112, fig. 1), are groups of thick-walled hypodermal cells, probably of a fibrous nature. These lie at rather regular intervals, presumably between the rows of stomata.

EXPLANATION OF PLATE 109

All specimens from Shippard's Chine, Isle of Wight.

Figs. 1, 2. *Pseudofrenelopsis parceramosa* (Fontaine) Watson (Fusain Type I). 1. T.L.S. showing partially biseriate ray. × 550. 2. T.L.S. showing typical rays and some tangential pitting.

Figs. 3–8. Fusain Type II. 3. T.S. showing growth rings. × 120. 4. T.L.S. showing part of a ray with cross-field pits sectioned by fracture plane. × 1800. 5. T.L.S. showing both ray cells and a tracheid with deposits in the lumina. × 750. 6, 7. Typical tracheid pitting seen in R.L.S. 6, × 500; 7, × 250. 8. R.L.S. with cross-field pitting seen from the tracheid side.



ALVIN *et al.*, *Pseudofrenelopsis* and Fusain Type II

The pith is about 1 mm in diameter and consists of thin walled cells 90–170 μm in diameter and about 2–3 times as long as broad (Pl. 112, figs. 2, 3, 6). The cells are round or polygonal in transverse section and without intercellular spaces.

The xylem cylinder is about 0·4 mm thick and consists of radially seriated tracheids and rays (Pl. 111, fig. 5). There is no indication of a growth ring. Primary xylem of scalariform tracheids, 8–13 μm in diameter, is seen adjacent to the pith (Pl. 111, fig. 6).

Secondary wood tracheids have rounded lumina and are relatively thick walled, 5–15 μm in diameter with walls 1·0–1·5 μm thick. The bordered pits on the radial walls are uniseriate and generally contiguous (Pl. 111, fig. 7; Pl. 112, fig. 4). Few rays were observed in the 3 mm long portion fractured longitudinally; they are 2–3 cells high and consist of thin walled parenchyma cells about 40 μm long, 20 μm high. The cross-field areas vary in shape from vertically elongated (near the pith) to square; they contain 3–11 round, cupressoid pits, 4–5 μm in diameter with obliquely orientated apertures about 1·0 × 1·5 μm. The pits are slightly spaced and arranged in horizontal rows (Pl. 112, fig. 5). There are typically 3–4 rows of two or three pits in the broader fields, but in high, narrow fields near the pith there may sometimes be only a single vertical row.

Comments. The morphology and cuticle of the *Pseudofrenelopsis* shoot, well known from previous work (Watson, 1977), demonstrate that the stem was photosynthetic and had highly xeromorphic epidermal features. The internal anatomy shows nothing especially remarkable. Chief interest lies in the wood and its resemblance to the silicified cores of major axes and Type I of the fusain. The tracheid and cross-field pitting is of the same kind, though somewhat smaller. The tracheids themselves are smaller and thinner walled and the cross-fields tend to be narrower with somewhat fewer pits in the horizontal rows. This difference in the cross-field is especially marked near the pith. Such variations in size and proportion might be expected between a slender twig and a main branch or trunk (Schweingruber 1978). The only quantitative differences are the absence of growth rings and of septate tracheids. The absence of any growth ring in the twig almost certainly means that it grew entirely within one growing period. Septate tracheids are of local occurrence in the silicified and fusainized wood and appear always to be associated with the late wood.

We therefore have little hesitation in identifying the wood we have described from silicified cores of major axes and from fusain samples as belonging to *Pseudofrenelopsis parceramosa.*

4. *Compressed wood and decorticated twigs*

Such material will often fracture successfully in the median longitudinal plane of compression and may reveal some aspects of wood anatomy. The several specimens of this kind from the Shippard's Chine deposit which we have examined have all agreed with the *Pseudofrenelopsis* wood in tracheid pitting (Pl. 110, fig. 6). A few specimens have also revealed the typical cross-field pitting (Pl. 110, fig. 7). Thus some evidence is provided that this debris of decorticated twigs and compressed wood may largely represent the same conifer.

THE 'PINE RAFT' MATERIAL

Microscopical preparations have been made from two permineralized logs and six pieces of fusain. Both of the logs were poorly preserved, though one which was sampled at several places across a transverse plane showed slightly better preservation in some areas. Enough structure was revealed to enable us to conclude that the two

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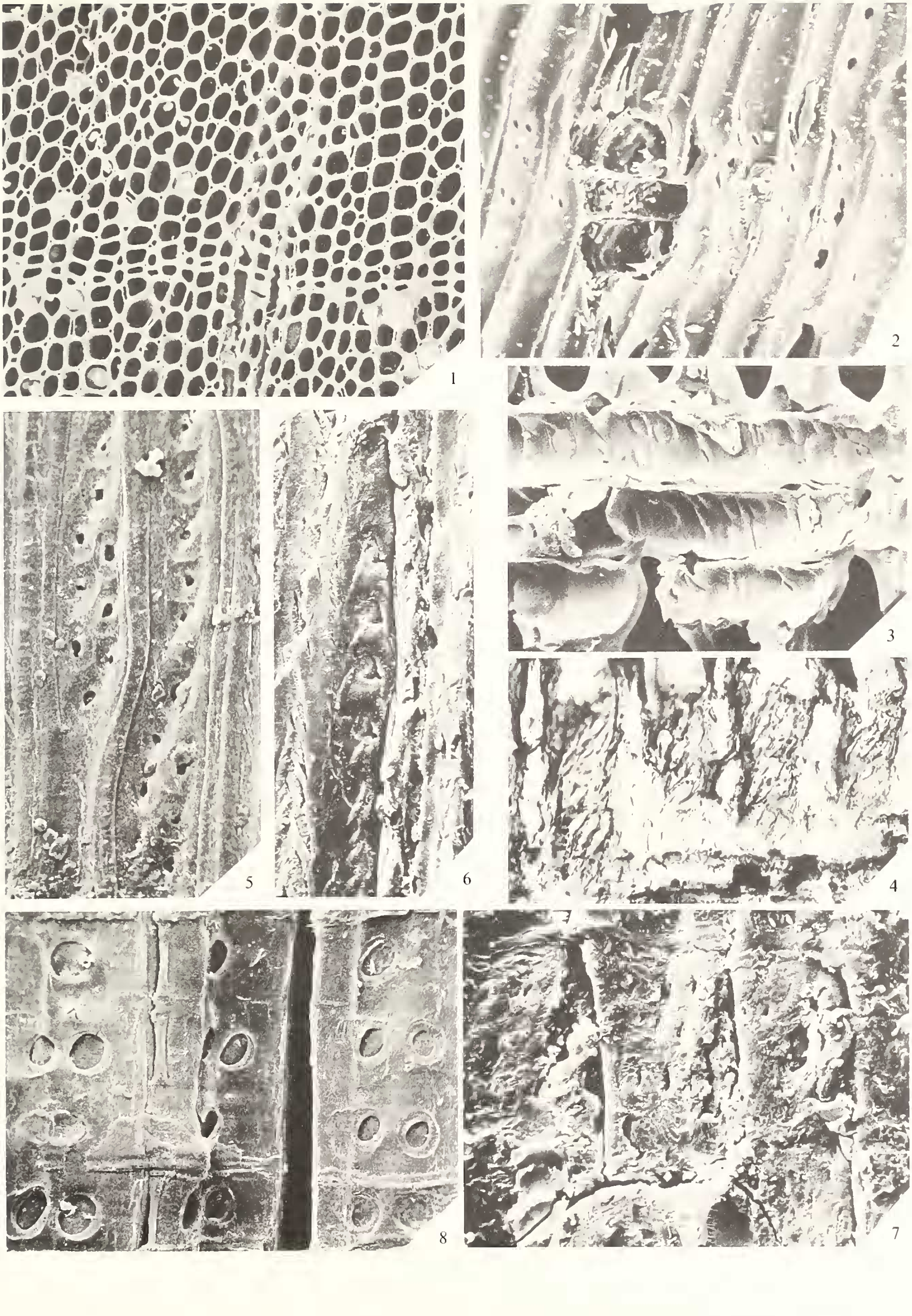
EXPLANATION OF PLATE 110

Figs. 1–3, 6, 7 from Shippard's Chine, Isle of Wight.
Figs. 4, 5, 8 from Hanover Point, Isle of Wight.
Figs. 1–3. Fusain Type III. 1. T.S. at growth ring. × 200. 2. R.L.S. with cross-field pitting seen from the tracheid side. × 560. 3. R.L.S. showing fractured ray with cross-field pitting seen from ray cell side. × 1100.
Figs. 4, 5. Pine Raft material. 4. R.L.S. of Pine Raft mineralized wood showing poorly preserved cross-field pits. × 500. 5. R.L.S. of fusainized specimen of the same kind of wood showing tracheid pitting.
Figs. 6, 7. Compressed twigs, believed to belong to *Pseudofrenelopsis parceramosa*, in R.L.S. fracture. 6, showing tracheid pitting. × 550. 7, showing an indication of cross-field pitting. × 1100.
Fig. 8. R.L.S. of a fusain specimen from the Pine Raft matrix showing cross-field pitting. × 680.



ALVIN *et al.*, Fusain Type III, Pine Raft Material and *Pseudofrenelopsis* logs were probably identical in anatomy and certainly different from any of the woods examined from the Shippard's Chine site. The tracheid pitting is similar in character to that of *Pseudofrenelopsis* in being typically contiguous, but differs in the much more frequent occurrence of a biseriate-alternate arrangement. It is so much more araucaroid in character that it would probably be classifiable in the form-genus *Dadoxylon* Endlicher. The cross-field pits, so far as we have been able to determine, seem to be of the same character, but there are fewer per field (Pl. 110, fig. 4). Due to the poor preservation it is not clear if the growth rings are comparable: macroscopically rings are marked, but details cannot be seen clearly in the microscope. Ray height is greater than in the *Pseudofrenelopsis* wood, the cell number ranging from 2–15 (mode 10, 65% 5–10) cells.

The fusainized wood debris present locally in the pine raft matrix has been sampled only in a preliminary way. Of the six specimens examined, four showed the tracheid pitting characters of the pine raft wood (Pl. 110, fig. 5); these specimens showed also the cross-field pitting in a better state of preservation. The other two specimens represented different kinds of woods, one being similar, but not identical to the Type II fusain at the Shippard's Chine site (Pl. 110, fig. 8).

GENERAL DISCUSSION

1. *Wood anatomy of Cheirolepidiaceae*

In his summary of the characteristics of this family, Harris (1979), on the basis of his own earlier observations on material of *Hirmeriella* from South Wales (Harris, 1957) and of those of Vogellehner (1965), states that the wood is of the *Protocupressinoxylon* type. The distinction between *Protocupressinoxylon* and *Protopodocarpoxylon* is not, however, very fundamental, resting chiefly on the different number and arrangement of the cross-field pits. Like several other form-genera of Mesozoic woods, they share the semi-araucaroid or protopinaceous tracheid pitting.

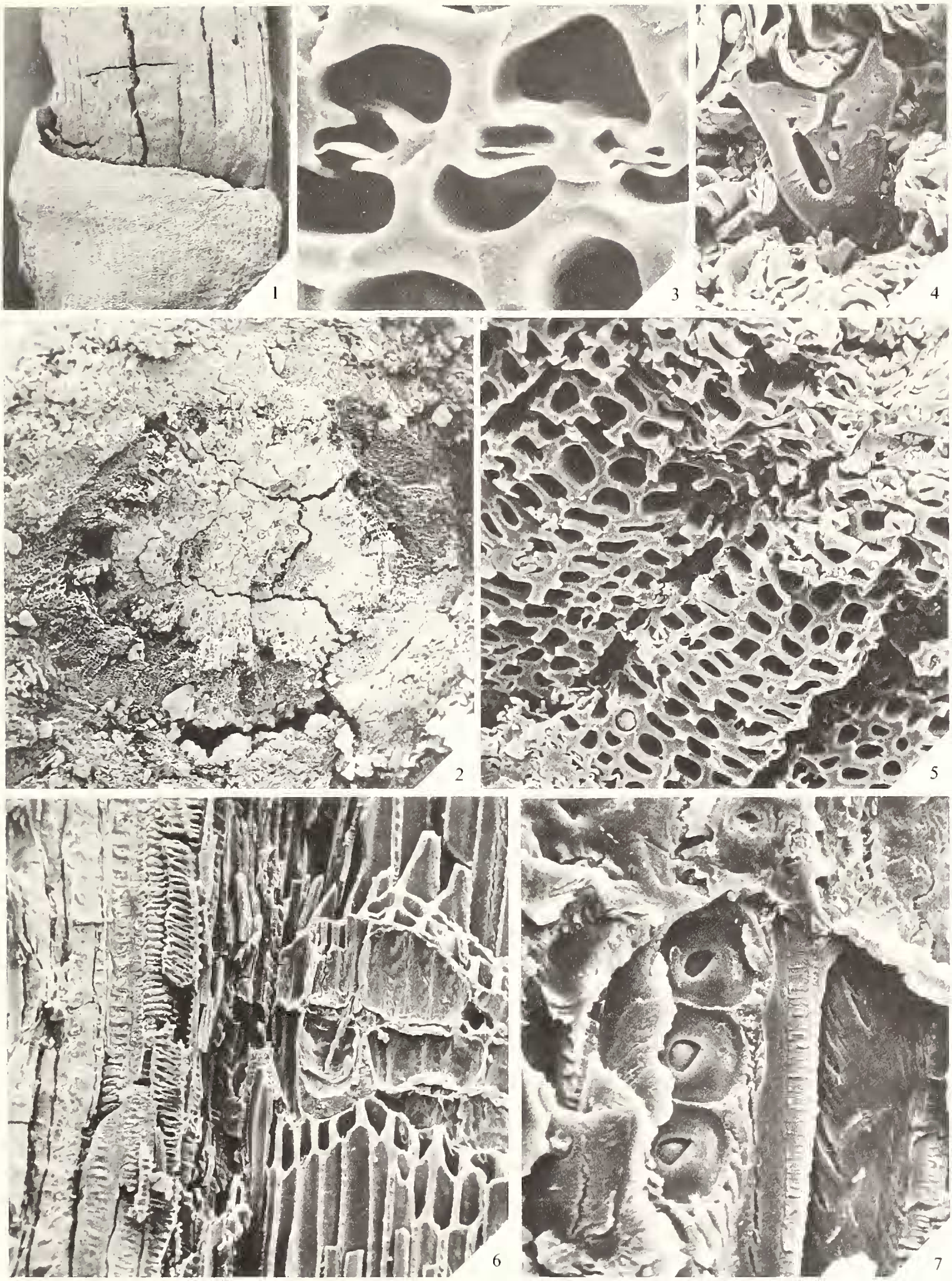
Recently, Lauverjat and Pons (1978) have described the anatomy of a well-preserved wood from Portugal which they name *Protopodocarpoxylon aveiroense* and which, on the basis of association, they attribute to *Frenelopsis oligostomata* Romariz. This wood has much in common with the wood we here attribute to *Pseudofrenelopsis parceramosa*: the cross-field and tracheid pitting is remarkably similar as also are the cell number and structure of the rays. The chief differences are the presence of specialized, narrow resin cells in the rays in the Portuguese wood and the absence of septate tracheids. Septate tracheids, however, are rare in our wood and confined to the vicinity of the late wood.

A general septate condition of the tracheids was reported for the genus *Embergerixylon* Lemoigne (1968*a*), species of which, according to Lemoigne (1970, 1972), have other characters in common including again the semi-araucaroid tracheid pitting and possibly also the possession of one or two large, podocarpoid pits in the cross-field. Lemoigne expressed the view that this probably represented a natural group of late Jurassic and Early Cretaceous conifers. The presence of some septate tracheids in our *Pseudofrenelopsis* wood perhaps suggests that *Embergerixylon* may have some affinity with Cheirolepidiaceae, but the true status and characters of *Embergerixylon* are not clear.

The wood of *Brachyphyllum desnoyersii* (Brongniart) Saporta from the Callovian of the Cote d'Or, described by Lemoigne (1968*b*) again has the semi-araucaroid tracheid pitting and cross-field pitting of *Protopodocarpoxylon* and septate tracheids are also sometimes present. Lemoigne attributes this wood to *Brachyoxylon* Hollick and Jeffrey (1909) although this genus is distinguished by the presence

EXPLANATION OF PLATE 111

Specimen from Shippard's Chine, Isle of Wight. *Pseudofenelopsis parceramosa* (Fontaine) Watson. 1. Twig showing typical node. V60207. ×10. 2. Cross fracture showing pith, woody cylinder and part of cortex. V60207. ×40. 3. Portion of woody cylinder showing homogeneous walls indicative of fusain, with fractured tracheid pits two of which show clear tori. V60207. ×2420. 4. Possible stone cells in otherwise shattered thin-walled cells of cortex. V60207. ×600. 5. Woody cylinder showing some shattering and compaction at top-right. V60207. ×450. 6. R.L.S. fracture showing part of pith (left), primary xylem and secondary wood (right). V60208. ×520. 7. R.L.S. fracture through wood showing contiguous pitting (in plane of middle lamella) and tracheid walls with evidence of decay. V60208. ×2000.



ALVIN *et al.*, *Pseudofrenelopsis*

of traumatic resin canals. *Brachyoxylon* was erected by Hollick and Jeffrey for a species, *B. notabile*, believed to be the wood of *Brachyphyllum macrocarpum* Newberry from the Lower Cretaceous of Kreischerville, Staten Island. *Brachyoxylon brachyphylloides* (Torrey) Kräusel, reported from both the Middle Jurassic and the Lower Cretaceous (Lemoigne, 1972) has septate tracheids in the late wood, but more abundantly than in *Pseudofrenelopsis*.

Table 2 summarizes the attribution of wood types to Cheirolepidiaceae. All have the following features in common: (1) tracheid pitting of the semi-araucaroid type (*type mixte* of French workers); (2) cross-field pitting of several to numerous cupressoid pits; (3) absence of vertical parenchyma, but resinous tracheids often present; (4) ray cells with resinous deposits.

TABLE 2. Woods of Cheirolepidiaceae or probable Cheirolepidiaceae

Species	Locality	Age	Wood type
Cheirolepidiaceae			
Hirmeriella muensteri (Schenk) Jung (or possibly *H. airelensis* Muir and Konijnenburg-van Cittert (1971)	S. Wales	L. Jurassic	*Protocupressinoxylon*
Frenelopsis oligostomata Romariz	Portugal	U. Cretaceous	**Protopodocarpoxylon*
Pseudofrenelopsis parceramosa (Fontaine) Watson	S. England	L. Cretaceous	*Protopodocarpoxylon*
Probable Cheirolepidiaceae			
Brachyphyllum desnoyersii (Brongniart) Saporta	France	M. Jurassic	'*Brachyoxylon*' (but without traumatic resin canals) (= ?*Protopodocarpoxylon*)
B. macrocarpum Newberry	New York, U.S.A.	L. Cretaceous	*Brachyoxylon*

* Attributed on basis of association.

Numerous Jurassic and Cretaceous woods have been described with this combination of characters and several other form-genera of Mesozoic woods, of which nothing is known of their botanical affinities, possess the semi-araucaroid tracheid pitting. These woods together constitute Kräusel's (1949) Protopinaceae. The status of this group and the significance of its abundance in the Mesozoic have been much discussed, a useful summary of views having been published by Lemoigne (1972). It is of interest that the few Cheirolepidiaceae in which the wood is now known should all have the protopinaceous tracheid pitting, but these examples represent only a very small range of the characters found within this very large assemblage of wood types.

EXPLANATION OF PLATE 112

Specimen from Shippard's Chine, Isle of Wight. *Pseudofrenelopsis parceramosa* (Fontaine) Watson. 1. Cross fracture showing epidermis with thick outer walls and (right) group of hypodermal fibres. V60207. ×900. 2. Cross fracture showing part of mineralized pith and woody cylinder. V60207. ×190. 3. The same in longitudinal fracture. V60208. ×190. 4. R.L.S. showing typical pitting. V60208. ×800. 5. R.L.S. showing cross-field pitting from ray cell side and possible fungal hyphae. V60208. ×1600. 6. Cross fracture of pith showing iron pyrites-filled cells. V60207. ×900.

ALVIN *et al.*, *Pseudofrenelopsis*

2. *Palaeoecology of* Pseudofrenelopsis

If, as we believe, the anatomical differences between the structurally preserved *Pseudofrenelopsis* twig and the silicified wood are explainable in terms of 'juvenile' and more 'mature' wood, then we must conclude that this conifer formed a massive tree with trunks up to some 70 cm in diameter. It is therefore likely to have been a forest tree rather than a scrubby or sub-herbaceous plant such as the possibly cheirolepidiaceous *Brachyphyllum nepos* Saporta described by Jung (1974) from the Upper Jurassic of southern Germany.

Oldham (1976), in his study of the plant debris beds in the English Wealden concluded from the great abundance and high frequency of remains of this conifer, that it probably dominated river margin swamps. Our field observations are not inconsistent with that view (see below). The photosynthetic organs of the plant, i.e. the ultimate shoots with their thickly cutinized stems and extremely reduced leaves, seem well adapted to conditions of high insolation and water stress. It is therefore conceivable that the *Pseudofrenelopsis* forest inhabited soils, the water availability of which was variable. The irregular growth rings of the wood may well be related to periods of drought when growth was interrupted. The prodigious quantity in our deposit of unbranched ultimate shoots of more or less uniform diameter suggests that only a small proportion of the new growth persisted to increase extension. The rest presumably dropped at the end of their useful life as photosynthetic organs in the same manner as the leaves or sometimes the shoots in most evergreen trees, including conifers, today (Harris, 1976). Shoot dropping could have been related to periods unfavourable to growth.

The current interpretation of the Wealden environment is that of a variable salinity coastal mudplain with lagoons and sandy braided river system (Allen, 1975). During Hauterivian–Barremian times intense weathering of source massifs has been suggested as necessary to account for the large quantity of sediment that gave rise to prolonged mudswamp conditions amongst the braided stream channels (Allen, 1975). The observed features of the Shippard's Chine deposit and that of the 'pine raft' fit well in this scheme.

The Shippard's Chine locality is interpreted as an abandoned stream channel, possibly a section of a braided river, in which water flow was variable. The poorly sorted silts and clays, together with the wood preservation of the plant material, suggest rapid sediment deposition. Flow in the channel was directional at least some of the time as evidenced by the orientation of some of the plant remains. The inclusion of apparently water-worn fusain suggests that not all the organic material was of immediate local origin. This implies a periodic connection with the main river system. The poor sorting of the plant debris and the preservation of comparatively delicate structures, however, provide evidence that the bulk of organic material was derived from vegetation growing near the site of deposition. Stream bank collapse during periods of increased flow would account for the mixture of debris, the composition of which is reminiscent of forest litter. Such concentrations of plant material have been observed in modern flood deposits in which extensive forest floor erosion is known to have occurred.

The upward fining of the inorganic sediments in the deposit indicates a reduction of flow intensity as the channel silted up culminating perhaps in the colonization of the sub-aerial sediments by plants and the formation of a soil horizon. Shallowing water depth would also account for the lack of inwashed logs in the upper bed. The presence of pyrite in the delicate slender twig with compression confined to the less robust tissues leads us to believe that pyritization occurred soon after burial and that the lower plant bed must have been in an anaerobic environment. The upper bed, however, exhibits some oxidation effects and little or no pyrite. The close proximity to a sub-aerial soil horizon could well account for this.

The pine raft locality is also considered to represent a channel deposit, but the sandier matrix and the more massive logs suggest that more vigorous conditions occurred.

The salinity of the depositional environment is difficult to determine. *Lepidotes mantelli* teeth occur in association with the plant beds at Shippard's Chine but this species is believed to occur in both fresh and marine waters. Undoubtedly, because of the presence of stream channels the conditions were non-marine but the possibility that the waters were brackish to some degree from time to time cannot be ruled out.

A warm wet environment has been postulated to account for the deep chemical weathering necessary to yield the volume of sediments of the type in the Wealden clay group (Allen, 1975). The growth rings observed in all the woods provide evidence of climatic seasonality or at least of fluctuation.

As the palaeolatitude for southern Britain during the Mid-Cretaceous was approximately 35 °KrN (Smith *et al.*, 1973), temperature is unlikely to have been the dominant fluctuating factor, but rather the extensive occurrence of fossil charcoal is indicative of pronounced dry periods during which forest fires were common as suggested by Batten (1975). The presence of widespread fossil mudcracks in other parts of the Wealden beds supports this (Allen, 1975).

However, the evidence of fungal decay in the woods necessitates the postulation of high humidity at least locally, and high rainfall during part of the year is required to maintain the extensive braided sand plains. The frequent presence of epiphyllous fungi on the *Pseudofrenelopsis* shoots also suggests high humidity at least at times or in some parts of the forest canopy (Alvin and Muir, 1970).

Among the suggestions based on palynological evidence concerning the palaeoecology of *Classopollis* producers in the Wealden is that the plants might have been mangrove-like (Batten, 1975). Abundant moisture was obviously present in the growth environment of *Pseudofrenelopsis* for much of the time, but acute water stress occurred occasionally when the trees could have ceased growing and become vulnerable to vegetational fires. Without additional evidence of evaporite beds, it is difficult to envisage this happening in a mangrove community. Rather we believe that *Pseudofrenelopsis* was a forest tree, possibly forming a canopy beneath which the associated cf. *Brachyphyllum obesum*, with its comparatively thin cuticle and non-sunken stomata, could have grown. It is impossible to say whether our Type II wood belonged to this conifer, but circumstantially it would seem not unlikely.

The 'Pine Raft' deposit could represent a similar community, dominated by a different conifer, but until further work is done on other debris beds, we cannot say how widespread or how diverse Wealden forest communities may have been.

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